between Zomba and Lake Chilwa. The horns measured about $29\frac{1}{2}$ inches in length, and were $16\frac{1}{2}$ inches apart at their upper ends.

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Col. L. H. Irby, F.Z.S., exhibited and made remarks on two specimens of the Greater Bullfinch (*Pyrrhula major*), killed on the coast of Yorkshire about 1st Nov., 1893.

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Mr. W. T. Blanford, F.R.S., exhibited and made remarks on specimens of the Siberian Ibex (*Capra sibirica*) and the Ammon Sheep (*Ovis ammon*), shot by Major Cumberland in the Altai Mountains.

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Mr. Swale Vincent, M.B. Lond., Demonstrator of Physiology and Histology, Mason's College, Birmingham, read a memoir entitled "Contributions to the Comparative Anatomy and Histology of the Suprarenal Capsules." This portion of the memoir dealt with the suprarenal bodies in Fishes and their relation to the so-called head-kidney.

This paper will be printed entire in the Society's 'Transactions.'

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The following papers were read:—

## 1. On the Complete or Partial Suppression of the Right Lung in the *Amphisbænidæ* and of the Left Lung in Snakes and Snake-like Lizards and Amphibians. By Gerard W. Butler, B.A., F.Z.S.

[Received June 14, 1895.]

(Plate XL.)

Contents.



### I. Introductory.

The absence of paired symmetry in the lungs of Snakes has been recognized from early times. Thus Aristotle [B.C. 384–322] describes Snakes (as known to him) as having but one lung[1]. We find this view repeated without qualification so late as 1805 in a work for which Cuvier is responsible[2].

It would seem that Nitzsch [1808] was the first to describe the rudiment of the second lung (which, be it noted, he rightly speaks of as the *left* lung) in the Common Snake (*Tropidonotus natrix*), and to suggest that this rudiment would probably be found in many other Snakes (**1**)[3].

Since 1808, thanks to such workers as Meckel, Cuvier, Duvernoy, Stannius, and Cope, our information on the subject has been largely augmented.

In a sense it may be said that, excluding details, there is little in this paper which has not been stated or hinted by some one previously. But it is equally true that there is little here which has not been as categorically denied by some one else of equal authority.

It has thus happened that an interesting generalization has so far been missed.

This is doubtless in part due to the fact that no one person has given special attention to the matter in all the groups of animals concerned, but in part also to error of interpretation, or error or looseness of description on the part of observers, and in part perhaps to want of caution on the part of compilers when summing up.

However this be, it seems well to have the facts placed clearly on record now.

When studying the pleuroperitoneal spaces and membranes of Lizards, Snakes, &c., in the years 1889–1892[4], I of course had to note the relations of the lungs, and I was much struck by the fact that whereas in the Amphisbænidæ it was always the right lung that was reduced or absent, in Snakes and in other Snake-like Lizards it was the left.

When I came to enquire what had previously been written on the subject, I found that there was no satisfactory summing up of the whole matter, and that so far as separate animals or groups of animals were concerned, while some previous statements harmonized with my observations, others of equal authority ran counter to them, while, thirdly, many writers did not commit themselves one way or the other. I have accordingly been over my old observations, and supplemented them by others, with the result of only confirming and widening the generalization at first arrived at, which is—[I of course speak only of the animals examined, see lists, § VI.]—that *the Amphisbænidæ stand alone*

[1] Aristotle's 'History of Animals' (R. Creswell's translation in H. G. Bohn's "Classical Library"), Book ii. chap. ii. § 12, p. 44 (London, 1862).

[2] 'Leçons d'Anatomie comparée de Georges Cuvier, recueillies et publiées sous ses yeux par G. L. Duvernoy,' tom. iv. pp. 323 & 347 (Paris, 1805).

[3] See Bibliography at the end of this paper. Throughout the paper the large numbers in brackets inserted in the text refer to the corresponding work in the list at the end.

[4] Proc. Zool. Soc. 1889, pp. 452–474, and 1892, pp. 477–498.

*among pulmonate vertebrates in having the right lung completely or partially suppressed.*

The observations recorded in this paper are of course not exhaustive, but I think the types examined make up a good representative set; and though it is of course not safe from a knowledge of the anatomy of nine animals to prophesy as to that of a tenth though apparently nearly related, still I think the probability is that if we open a specimen of any species of Amphisbænid we shall find the left lung well developed and the right lung smaller, rudimentary, or absent, and that in any other animal, if one lung is markedly smaller, rudimentary, or absent, it will be the left lung.

In itself the suppression of one lung rather than the other does not perhaps appear to be a characteristic of great significance; and if, as has been stated, it were a fact that some Snakes had the right lung rudimentary and some the left, the case would be different. If, however, as my observations so far as they go indicate, the suppression of the right lung is really confined to one family of animals, which are peculiar and interesting in other ways, it is surely a point worth noting, both for its own sake and because it may probably be indicative of some less superficial peculiarity in the plan of organization of these animals.

I may perhaps be able to follow up the matter some other time when I more fully understand the significance of certain other peculiarities of these animals. The main object of the present paper is to state the facts observed.

If any exceptions to the generalization above stated should be discovered [1], I should be much interested to hear of them. Such exceptions, if they exist, would not improbably be suggestive in one way or another. Let no one, however, after reading this paper speak of a rudimentary left lung in an Amphisbænid or a rudimentary right lung in a Snake or any animal other than an Amphisbænid until he has first carefully re-examined his specimen in the light of what follows.

For permission to examine a number of species of which I do not myself possess specimens my best thanks are due to my former teacher Prof. G. B. Howes, and secondly to Mr. G. A. Boulenger, F.R.S. The latter has also very kindly named my specimens in accordance with his latest edition of the British Museum Catalogues of Snakes and Lizards.

## II. A Review of previous Statements.

At the end of this paper will be found a list of the works which, so far as my knowledge goes, contain the most noteworthy

[1] For a discussion of the description and figure of the lungs of *Chirotes* by Cuvier and Flourens respectively, see below, pp. 694, 702.

I hope that anyone who has an opportunity of dissecting either *Chirotes* or any snake-like Lizards not mentioned in my lists will make an outline sketch of the heart, lungs, and liver, *in situ*, as seen from the ventral side, so as to show the relative size of the two lungs.

contributions to the subject herein discussed. I will here briefly allude to these and to a few other references of lesser importance, partly to do justice to the authors named, and partly to show cause for the publication of this present paper.

(i.) I have already referred to the work of Nitzsch [(1)]. His treatment of the matter is excellent, so far as it goes[1].

(ii.) J. F. Meckel [(2) p. 84], using of course an earlier system of classification in discussing the lungs of Snakes, noted correctly that in the Amphisbænidæ the rudimentary lung, if present, is on the right side, but he spoilt this observation by adding that this also was the case with all the "Colubers" he had examined [2]. He was again, however, right in saying that the smaller lung was on the left in all the Boas and *Tortrix scytale*, as well as in *Anguis fragilis*.

(iii.) In his later work [(3) pp. 259 & 260] he made another mistake in adding *Cœcilia*, as well as the Colubers, to the Amphisbænidæ as having the rudimentary lung on the right side. He was, however, right in placing *Platurus* and *Typhlops*, as well as the lizards *Ophisaurus*, *Pseudopus*, *Bipes*, and *Seps* with the Boas, *Tortrix*, and *Anguis* of his previous paper, as having the right lung the largest. As to *Chirotes*, which Amphisbænid, he avers, has the right lung much the largest, see below, pp. 702 & 703.

(iv.) The treatment of this subject in the second edition of Cuvier's 'Leçons d'Anatomie comparée' [(4)] shows in some respects a marked advance on the papers previously mentioned. Nevertheless, although we have details with regard to some

[1] Nitzsch, *l. c.* p. 13, after describing the lungs of Lizards, says that *Anguis fragilis* has the right lung rather longer than the left. He then describes the rudimentary left lung of *Tropidonotus* (*Coluber*) *natrix*:—

"In Colubro natrice autem sinistrum liberum, minimum, piso communi parum majorem, tamen cellulosum, dextrum contra maximum, longissimum . . . Quemadmodum vero in isto Colubro, ita in reliquis serpentibus, quibus auctores unum modo pulmonarem follem tribuunt, hoc organon comparatum [paired] esse autumaverim. Haud dubie sinister, quanquam minimus, vere adest. Non omnibus saltem serpentibus unum duntaxat pulmonem esse proposita exempla docent."

The expectation expressed in the last sentence but one is of course not fully borne out. There are a number of Snakes that have no trace of a second lung; but there are very many in which, as in *Tropidonotus natrix*, the left may be easily overlooked. I have thought it worth while to quote his words because he was apparently the first to describe this rudimentary left lung, because his description is so good, and because he at once grasped the fact that the rudimentary lung of such a Colubrine Snake is the left lung—a thing which has always seemed to me pretty obvious, but which has struck some other people differently.

[2] Meckel and Cope have used the terms "Colubern" and "Colubroidea" respectively [see (2) and (7)] in a wide sense almost co-extensive with the Linnean genus *Coluber*, so that under these headings come a large majority of known Snakes. This of course adds greatly to the importance of any general statement they make as to Colubers or Colubroidea. Further, if Meckel and Cope do not actually state that the rudimentary lung of these Snakes corresponds to the right lung of other animals, their writings tend to spread this view when, without further comment, they say that this rudimentary lung is "on the right side," or, as Cope, figure it as "right lung."

animals given with greater accuracy and preciseness [1], and have in different places hints that Duvernoy had noticed that it was the rule for the left lung to be rudimentary in Snakes [2], much is from our present point of view left vague [3], and there seems to be at least one error [4], which is sufficient to prevent him arriving at a correct generalization.

(v.) Stannius [(5)] errs in saying that the Amphisbænidæ agree with a number of other Snake-like Lizards which he mentions in having the left lung reduced [*l. c.* p. 206 and note]. As to Snakes, he mentions a number of kinds, and states whether they have more than one lung, but he does not say whether it is the right or left lung that is reduced.

(vi.) Milne-Edwards [(6)] gives a *résumé* with references to the literature of the subject. While, however (*l. c.* p. 308, note), he says that it is the left lung which is the smaller in Pythons, Boas, and Slowworm, and that it is the right which is rudimentary in Amphisbænidæ, at the top of the next page he says (speaking of Snakes) "l'atrophie du poumon porte tantôt à droite, tantôt à gauche."

(vii.) The recognized text-books and encyclopædic sources of

[1] Thus, on p. 37, Duvernoy rightly states that in Cæcilians the left lung (not the right, as Meckel had stated) is rudimentary, and on p. 38 gives exact measurements of the two lungs in different species of these Amphibians. On p. 32 he rightly repeats that the left lung of *Anguis fragilis* is the smaller.

[2] Thus, *l. c.* p. 33, after describing the lungs of *Eryx turcicus* [this should be a synonym of *Eryx jaculus*, L.], he adds, "Nous verrons dans les détails de la structure de ces deux sacs que le gauche répond au poumon rudimentaire des autres Ophidiens."

Again, on the same page, he describes the left lung as rudimentary in "l'Hétérodon tacheté" [*Heterodon platyrhinus*, Latr.], and, as will be noted below, p. 701, this is a Snake in whose case, if in any, it would be most natural to fall into the error of describing the rudimentary lung as the right.

Again on p. 36. After stating that there is no trace of a "second" lung in certain species of *Vipera* and other Snakes, he adds, "Mais il y a un rudiment du poumon gauche dans *l'Acanthophis tortor* . . ."—a passage which makes one think that though in various places he used the vague expression "deuxième poumon," he meant "poumon gauche."

[3] Thus on p. 32 we are told which lung is the smaller in *Pseudopus pallasii* [*Ophisaurus apus*, Pall.], *Ophisaurus ventralis*, and the Amphisbænidæ. In this 1840 edition of the 'Leçons,' as in the 1829 edition of the 'Règne Animal,' these snake-like forms are classed with the Snakes, and if, in accordance with the preceding note, we credit Duvernoy with recognizing that it is the left lung which is reduced or absent in Snakes, we must on the other hand note that he fails to remark that the Amphisbænidæ differ from Snakes and other snake-like forms in having the right, and not the left, lung reduced or rudimentary.

[4] On p. 28 we are told that "*Bipes lineatus*" has "le poumon droit moitié plus court que le gauche." Comparing this note with the corresponding passage of the 'Règne Animal' of 1829 (from which Duvernoy, in a note on p. 37, explains that he is quoting certain other statements), I gather (see 'Règne Animal,' 1829, tom. ii. p. 65) that he refers to *Scelotes bipes*, L. [Brit. Mus. Cat. Lizards, vol. iii. p. 414]; and if so he is mistaken, for this Lizard is no exception to the general rule, but has the right lung longer than the left.

I do not censure Duvernoy for making the not uncommon error of confusing right and left. But this error, to my mind, discounts the adjoining statement about the lungs of *Chirotes*, as to which see below, pp. 702 & 703.

information of still more recent date, so far as I have seen, either hardly touch upon the subject, or else do not convey a definite and correct impression of the whole matter[1].

(viii.) Lastly Cope [1894 (7) & (8)] has recently published two papers which touch on this subject. These are storehouses of facts, and except with reference to his treatment of this one point, so far as I have been over the same ground, I have very little to do beyond endorsing his statements. But just because his name carries such weight, his treatment of this point is one of the strongest justifications of the publication of this paper. It will, however, be best to defer further reference to these papers, and especially the accompanying figures, to the next section, where I justify the contrary view of the matter.

## III. On the Complete or Partial Suppression of the Left Lung in Snakes.

### (a) *On a means of distinguishing the Right Lung from the Left in Snakes.*

In deciding as to the homology of the lungs of Snakes, in which animals in most cases one is quite rudimentary if not absent altogether, Embryology is of course our surest and best guide when we are able to resort to it. Thus I have serial sections of a number of stages of *Tripodonotus natrix* which show the early development of the lungs from the first commencement of the shutting off (Lamprey fashion) from behind forwards of the œsophagus from the anlage of the lungs and from the trachea to a time when the lungs have attained a fair size. These show us that it is the left lung, and not the right, which is from the first smaller than the other, and which as the snake grows remains quite rudimentary. I have also early stages of *Zamenis gemonensis* which show in like manner that the functional lung of this second Colubrine also is the right lung.

As to those Snakes which in the adult show no trace of a second

[1] As examples of this later class, and in further justification of this paper, not in any spirit of ungrateful criticism, I may refer to the fullest accounts of the subject that I have come across in the works of this type most familiar to English students.

*a.* Wiedersheim ['Lehrbuch der vergleichenden Anatomie der Wirbelthiere,' 2nd ed. p. 650, Jena, 1886] speaks of "die Lungen der Ophidier, wovon sich haüfig, ganz wie bei Gymnophionen und Amphisbænen, nur die eine, und zwar die rechte entwickelt, während die linke entweder ganz schwindet, oder doch meist nur sehr rudimentär erscheint."

The words, taken by themselves, do not necessarily mean that in the Amphisbænians it is the right lung that is well developed, but I think they naturally tend to produce that impression, especially in the mind of the reader who is sufficiently interested in the matter to look up the figures of *Siphonops* (*l. c.* fig. 454, p. 585) and *Amphisbæna* (*l. c.* fig. 459, p. 589), for the lung of the latter is there drawn to the right of the trachea and otherwise in the position of a right lung.

*b.* Hoffmann, in Bronn's 'Klassen und Ordnungen des Thierreichs,' Bd. vi. Abth. iii. p. 1594 [in a part dated 1886], is responsible for almost precisely the same words as those used by Wiedersheim.

lung, the embryological evidence, judging by the forms I have been able to study, is not so clear, because I have found no trace of more than one lung from the first. Thus in *Vipera aspis* and *Typhlops lumbricalis* I have stages which show the lung from an early stage inclining to the right side, after the manner of the right lung in the corresponding stages of such a form as *Tropidonotus natrix*, but there is no trace of a left lung.

In the case of many morphological questions, it is considered sufficient to study the development of a single typical species. But in the present case this is not so; for my gainsayers represent that in some Snakes one lung is developed, and in some the other. Now embryological evidence is of course the most convincing, but it is manifestly hopeless to think of studying the development of the lungs of every species of Snake, and, in the absence of embryological evidence, that of comparative anatomy is quite cogent enough I think for our present purpose. I therefore propose to show how we may easily tell the right lung from the left in any grown Snake by the light of comparative anatomy.

In most pulmonate vertebrates there can of course be no doubt as to which is the right and which the left lung, for the two lungs hang in separate lateral portions of the body-cavity, separated from each other by one or, more usually, by two membranous septa. There can be no question about the matter in the case of Amphisbænians and other Lizards, and any discordant statements about the lungs of these animals must be simply the result of a mistake, whether on the part of the observer, the compiler, or the printer.

With Snakes, however, it is otherwise. In Snakes as we know[1] the body-cavity is in its anterior region obliterated except for the pericardium and the two sacs which encase the right and left halves of the liver; and moreover the viscera show a displacement of a more or less rotatory character. It thus happens that though, in the great majority of cases, the rudimentary lung, if present, will be found just where, after seeing the rudimentary lungs of snake-like lizards and of Gymnophiona, and also on embryological grounds, we should expect to find the rudiment of the left lung of a Snake—[viz. on the left posterior border of the heart]—still there are a few species, e. g. *Heterodon platyrhinus* [see (7) pl. xv. or (8) pl. xxviii., and figs. 1–4 of this paper], in which first appearances are somewhat deceptive, so far as the rudimentary lung is concerned. In like manner, though the larger, more dorsally situated lung which Cope speaks of as the "left lung" has in most cases, to myself personally, appeared pretty clearly to be the right lung, still in many cases the position of this lung is so far median, or partly inclining to the right and partly to the left side of the animal, that an observer whose studies had not led him to investigate closely the relations of the organs in these animals might be in doubt. Yet once looked at the right way, the lungs of Snakes present hardly more difficulty than the lungs of Lizards and Amphibians.

[1] *Cf.* Proc. Zool. Soc. 1892, pp. 477–498.

As remarked above, and as is well known, the lungs of vertebrates are separated by one or more longitudinal septa. One of these contains the alimentary canal and is the median septum, marking the median plane of the body. This is composed of the dorsal ligament of the alimentary canal, the gastrohepatic and hepato-œsophageal membrane, and the ventral, or so-called "suspensory," ligament of the liver. The other membrane is that one which is so conspicuous in tailed Amphibians and most Lizards, passing from the dorsal surface of the right liver-lobe to the dorsal body-wall. This membrane which, with its fellow on the left side [which, however, except in Amphisbænidæ remains almost or quite rudimentary, owing apparently to the mechanical obstacle to its development offered by the laterally displaced stomach], can be traced either in the adults or the embryos of other pulmonate vertebrates, has under one name or another received much attention from those who in the last seven years have written on the membranes and septa of the vertebrate body-cavity [1]. We may, following Hochstetter, call it the "Hohlvenengekröse" (postcaval ligament), to express the idea that its hinder portion serves as a bridge for the posthepatic portion of the postcaval vein; or we may call it the "right pulmohepatic ligament," to express the idea that it, like its fellow of the other side when present, arises in the embryo [I speak of Amniota,—*Lacerta* and *Gallus*] in connection with the development of the lung and serves to attach it to the liver; or we may call it simply the right dorsal ligament of the liver. As a matter of fact this membrane, with the exception of its posterior portion, does not occur in Snakes as a membrane distinct from the median or gastrohepatic, for the body-cavity does not extend between the right lung and the œsophagus and stomach as in Amphibia and most Lizards. It is, however, well seen in many snake-like Lizards.

I have referred to these membranous septa because, as is so often the case with such membranes, they are the carriers of certain definite blood-vessels, which are to serve us as landmarks. The morphological position of these blood-vessels in relation to the various organs, and particularly to the lungs, we first of all fix by the fact of their running in these membranes, whose relations are so well known and clear in Lizards, and we then can use these same blood-vessels as landmarks in Snakes, where the membranous septa would otherwise be hardly traceable.

Fortunately for our purpose, in Snakes, as in some elongated snake-like Lizards and Amphibians, the blood-vessels referred to tend to occur as series of simple vessels instead of as a lesser number

[1] F. Hochstetter, "Ueber das Gekröse der hinteren Hohlvene," Anat. Anz. Bd. iii. pp. 965–974 (1888).

Ravn, Archiv für Anat. u. Phys., Anat. Abth. 1889, pp. 123–154 & 412.

G. W. Butler, Proc. Zool. Soc. 1889, pp. 452–474.

H. Klaatsch, "Zur Morphologie der Mesenterialbildungen am Darmkanal der Wirbelthiere. Theil I. Amphibien u. Reptilien," Morph. Jahrb. 1892, pp. 385–450.

of larger branched vessels, and running as they do in a dorso-ventral direction they, so to speak, constitute a double or treble palisade between the two lungs [or to the left or right of the one lung which may be present].

Thus, *firstly*, the aorta gives off dorsalwards a whole series of vertebro-intercostal arteries to the vertebral column and adjoining body-wall, and ventralwards arteries to the œsophagus and stomach, while from these a series of veins passes to the portal system of the liver. With the exception of a few Amphisbænidæ, in which all or part of the last-mentioned veins run in the right dorsal hepatic ligament[1], all the above-mentioned blood-vessels run in the median septum; and it will be seen that they form a well-marked palisade of vessels across the space between the mid-dorsal line of the liver and the vertebral column.

*Secondly*, starting from the aorta, we have arteries passing direct to the liver.

*Thirdly*, in a number of elongated snake-like Lizards [as was, I believe, first described for Lizards by Hochstetter[2] in *Anguis* and *Pseudopus* (*Ophisaurus*)] we find that the main part of the vertebro-intercostal blood of the hepatic region of the trunk is returned by a series of veins that run from the dorsal body-wall to the liver *via* its right dorsal ligament[3].

Now we find all of these above-mentioned series of blood-vessels fully developed in Snakes throughout the entire liver-region, as was admirably described by Schlemm[4] as early as 1826; and they show us that the larger, or only functional, lung of Snakes is the right lung.

[1] *E. g.* in *Amphisbæna* and *Lepidosternon* most or all of the veins from the œsophagus and anterior part of stomach run in the right ligament, which of course in these cases joins the alimentary canal. In *Blanus cinereus* part of the veins run in the right and part in the median ligament; while in the "Emphyodont" *Pachycalamus* and *Trogonophis* the veins run, as is, so far as I am aware, the rule for all other vertebrates, in the median membrane.

[2] F. Hochstetter, "Beiträge zur Entwicklungsgeschichte des Venensystems der Amnioten. II. Reptilien," Morph. Jahrb. Bd. xix. Heft 3, pp. 428–501, pls. xv.–xvii., Dec. 1892.

[3] I find these veins running in the right dorsal ligament of the liver in *Scelotes*, *Lygosoma*, *Lialis*, and various *Amphisbænidæ*, e. g. *Amphisbæna*, *Lepidosternon*, *Pachycalamus*, and they doubtless occur in the other snake-like Lizards examined. There may be as many as five, as in *Amphisbæna*, and perhaps more, spaced throughout the whole length of the liver.

A well-marked series of corresponding vessels is seen in *Amphiuma* and also in *Ichthyophis*, though in the last case they do not spring so directly from the vertebral column, but arise, as Hochstetter says has been described by Semon, from the unpaired vein between the mesonephric excretory organs which comes to take the place of the posterior cardinals of that region.

[4] Fried. Schlemm, "Anatomische Beschreibung des Blutgefässystems der Schlangen," Zeitschrift für Physiologie (Ed. G. R. & L. Ch. Treviranus), Bd. ii. pp. 101–124, pl. vii. (Darmstadt, 1826). See especially pp. 115, 121 & 122. On p. 121 he notices the series of vertebro-intercostal veins flowing into the portal vein in the liver, which were so commonly omitted in the descriptions published between 1826 and Hochstetter's paper of 1892, while curiously the comparatively insignificant, but, if I may so say, orthodox, vein that brings back blood from the first few postcardiac segments was always duly noticed.

When, as is commonly the case, the various longitudinally disposed viscera (the alimentary canal, liver, lung, and the longitudinal vascular trunks) between which they run are displaced from the positions they occupy in other animals, the course of these vessels is correspondingly circuitous. In fact, as the figures [Pl. XL. figs. 2–9], show, in passing from the vertebral column to the mid-dorsal line of the liver, they frequently have to describe a semicircle to pass round the mesial or left side of the larger right lung, which commonly encroaches considerably on the left half of the body.

Without very careful dissection the student may not in every uninjected spirit-specimen that comes into his hands find all the blood-vessels above referred to. I have not done so myself. In some cases I have found them all; in others now some series of vessels, now others; but in all the Snakes in my list I have obtained sufficient evidence from the blood-vessels to make it clear that the larger or only lung is the homologue of the right lung of other vertebrates.

(b) *Some Remarks on Prof. Cope's Papers on the Lungs of Snakes.*

Having thus presented what I believe to be without any shadow of doubt the correct view of the matter, and pointed out a simple means by which anyone may test the truth for himself, I think all that remains for me to do further is to explain away the apparently conflicting evidence of the figures in Prof. Cope's papers above mentioned [(7) and (8)]. I say the conflicting evidence of his figures, because in more than one place [(7) pp. 218 and 219, and (8) pp. 836 and 838] Prof. Cope expresses himself so as to suggest that he did not wish to commit himself to a use of the terms "right" and "left" in a morphological sense, but that he rather wished to designate those lungs which [in his opinion] are situated more to the right or left side of the animal. But when in his figures he labels the lungs R.L. and L.L. respectively, and in his explanation of the plates states that these letters stand for right lung and left lung, I think that the reader does carry away the impression that by these he means the lungs which are the homologues of the right and left lungs of other animals; and this impression will be deepened by certain passages in the papers [*e.g.* (7) p. 223 and (8) p. 838].

Now if we except *Typhlops* [(7) pl. xi.], which is one of the very few Snakes in which Cope will allow the "left" lung to be absent or smaller than the "right," we find that Cope in all his plates calls the best developed lung the "Left" lung and the smaller or rudimentary one the "Right"; and thus his figures are, as they stand, decidedly misleading.

While saying this I would, however, cordially acknowledge that the figures appear to have been carefully and truthfully drawn from the dissections, and such being the case, a comparatively brief cross examination of the figures brings out the truth.

Those who have carefully dissected this part of Snakes, and doubtless Prof. Cope himself among the first, will admit that the animals represented in (7) pls. xii., xiii., xiv., xv., and xvi., must have been prepared for sketching by cutting through the membranous tissue that connects the alimentary canal with the mid-dorsal line of the liver (and carries veins from the alimentary canal to the liver), and also the membranous tissue which passes to the right of the alimentary canal and attaches the liver to the dorsal body-wall and bears other blood-vessels to the liver; and will see that after cutting of these dorsal attachments of the liver that organ has either been merely pushed aside, as in pls. xiii. and xiv., or on the other hand has been turned over bodily through some 180 degrees, as in pls. xii., xv., and xvi. In either case the position of the lung with regard to the liver is not the natural one, and the impression is conveyed that the lung lies more to the left of the median plane than it really does.

That the membranes have been cut through, and the liver displaced as described, will, as remarked, be granted by those who have carefully studied this region of the snake's body, because of the unnatural position of the liver; but the displacement with inversion through some 180°, in the case of the snakes figured on plates xv. and xvi., will be recognized by all who remember that in Snakes, as in other animals, the postcaval vein enters the right half of the liver and not the left. The figures, in fact, are drawn in all good faith and tell their tale truthfully when carefully questioned, but the lettering and their appearance on the face of them are misleading.

The most striking figure is that of *Charina bottæ* [*l. c.* plate xii.] [one of the more normal two-lunged forms], where, after cutting through the dorsal attachments of the liver, the lungs and liver have evidently been turned over together in one piece to the right, so that the lungs lie ventral to the liver, with the larger right lung on the left and described as the left, and the smaller left lung on the right and described as the right.

We may now turn to consider the case of *Heterodon platyrhinus* [the curious forward diverticulum of whose chief lung has long been known[1]]. Cope figures this snake in both of his papers (7) pl. xv. and (8) pl. xxviii., and on account of its special interest in another respect I figure part of it here also [Pl. XL. fig. 1].

In this snake the position of the rudimentary lung with regard to the other, which is just as represented in Cope's figure, is at first view very deceptive.

It will be seen that the smaller rudimentary lung lies ventral to the other and to the right of the trachea. Not only, however, does the position of the larger lung with regard to the other organs, and notably to the blood-vessels above mentioned, prove that larger lung to be the right lung, but sections [see figs. 2–4], showing as they do a corresponding rotatory displacement of the

[1] See Duvernoy, 'Leçons d'Anat. comp. de G. Cuvier,' 2nd ed. tom. vii. p. 138 (1840).

organs (œsophagus, and aortic roots, &c.), explain the deceptive position of the rudimentary left lung.

Only one or two Snakes among those which I have examined are so deceptive as *Heterodon platyrhinus*, in the matter of the situation of the rudimentary lung, and none more so; and thus, having explained this case, I need not, I think, discuss any others, since all those that have come under my notice can be explained in the same way.

I give, however, a few other figures [figs. 5–9] of sections through different Snakes to show the kind of displacement of the viscera one finds, and to show how what is morphologically the median plane is indicated by the blood-vessels.

On referring to the figures we note that the characteristic displacements are—(1) of the right lung from the right side into a dorsal position underlying the vertebral column and extending more or less into the left half of the body, and, corresponding to this, displacements (2) of the œsophagus along the left side ventralwards, (3) of the aorta to the left side, and (4) of the liver towards the right side.

### IV. On the Complete or Partial Suppression of the Right Lung in Amphisbænidæ.

A reference to the list on p. 706 (which includes species of all the genera of *Amphisbænidæ* in the British Museum Catalogue, with the exception of the rare forms *Chirotes*, *Rhineura*, and *Agamedon*) shows that with the exception of *Trogonophis wiegmanni*, and to a lesser extent of *Pachycalamus brevis*, the right lung is rudimentary or absent altogether in all the Amphisbænidæ examined, while in these two it is distinctly smaller than the left. So far, then, as my observations go, this would seem to be a characteristic peculiarity of the Amphisbænidæ.

As to *Chirotes*[1] two writers[2] have made themselves responsible for the statement that the right lung is much larger than the left; while a third[3] has given a figure of the lungs apart from the other organs, in which the larger lung is called the right. This evidence would at first sight seem to settle the matter, and of course it is quite possible that the published view is correct. As *Chirotes* differs markedly from the other Amphisbænidæ in its possession of fore limbs, why, it may be said, should it not differ in respect of its lungs? Nevertheless, if, as seems indicated by its outward appearance, and as appears to be agreed by those who have studied its anatomy, *Chirotes* is an Amphisbænid, there is a certain pre-

[1] For a preliminary notice of a division of these animals into three genera, see Cope, "On the Genera and Species of Euchirotidæ," American Naturalist, May 1894, pp. 436–7 (figures in text).

[2] Meckel (3) p. 260; and Duvernoy (4) p. 28.

[3] P. Flourens, 'Mém. d'Anat. et de Phys. comp.—1. Études sur les lois de la symétrie dans le Règne Animal et sur la théorie du dédoublement organique,' Paris, 1884, pl. i. fig. 4.

sumption in favour of our finding the left lung the larger, so that I should like to know that the statements to the contrary were based on an inspection of the lungs *in situ* before considering the point decided [1].

## V. On the Smaller Size of the Left Lung in (1) certain Snake-like Lizards and Amphibians and (2) certain Mammals.

Having noticed that the Amphisbænidæ differed from Snakes in having their right lung, and not their left, reduced or absent, I was led to examine various other snake-like Lizards and Amphibians to see whether they in this respect agreed with the Amphisbænidæ or with the Snakes. A reference to the list given (p. 706) shows that I find that in all the lizards examined if one lung is smaller it is the left, and the same is true of the Gymnophiona examined, which is in accord with Wiedersheim's account based on more extensive acquaintance with this group.

Lastly, in many (according to some authorities in most [2]) mammals the right lung is larger than the left, sometimes considerably larger [3].

With the exception of Snakes, certain snake-like Lizards, Gymnophiona, and some mammals, all vertebrates, I believe, have both lungs well developed and either equal or differing but slightly in size; and the Amphisbænidæ appear to be the only animals in which the right lung is rudimentary.

[1] Specimens of *Chirotes* being scarce, our knowledge of the soft anatomy is probably derived chiefly from specimens which have been sacrificed to make skeletons, such organs as the lungs being put up separately in spirit. Of course descriptions based on such preparations would be unreliable as evidence on the point in question. Flourens's figure is ostensibly drawn from such a preparation; while that Meckel (and apparently Duvernoy also in one instance) has made incorrect statements as to the right and left lungs of other animals I have shown above (p. 694, and note 4 on p. 695).

There is, it seems, no dissected specimen of *Chirotes* in London. I have tried by writing to what seemed a likely quarter to ascertain whether there exists in Paris any preparation showing the visceral anatomy of *Chirotes*, but so far without success. It is to be hoped that anyone who is able to dissect this rare form will sketch the organs *in situ*.

[2] Thus G. L. Duvernoy, 'Leçons d'Anatomie comparée de Georges Cuvier,' 2nd ed. tom. vii. pp. 20, 24, 25 (Paris, 1840).

H. Milne-Edwards, 'Leçons sur la Physiologie et l'Anatomie comparée de l'Homme et des Animaux,' tom. ii. p. 334 (Paris, 1857).

[3] Thus the preparations exhibited at the Royal College of Surgeons show the right lung markedly the larger in *Talpa europæa*, *Mus decumanus*, *Notoryctes typhlops*, *Hyrax capensis*, *Synetheres* (*Cercolabes*) *mexicanus*, and less markedly so in various other mammals.

## VI. List of Species of Snakes and Snake-like Animals Examined.[1]

| | 1<br>Number of specimens examined. | 2<br>Larger Lung. | 3<br>Length of the Smaller Lung, that of the larger being taken as unity.[3] | |
|---|---|---|---|---|
| **OPHIDIA.**[2] | | | | |
| Fam. I. Typhlopidæ. | | | | |
| Typhlops lumbricalis, *L.* | 2 & Em. | R. | —— | |
| „ sp. | 1 | R. | —— | |
| „ sp. | 1 | R. | —— | |
| Fam. II. Glauconidæ. | | | | |
| Glauconia albifrons, *Wagl.* | 1 | R. | —— | * |
| Fam. III. Boidæ. | | | | |
| Subfam. 1. *Pythoninæ.* | | | | |
| Python molurus, *L.*, ♂ | 1 | R. | ·71. | * |
| „ „ ♀ | 1 | R. | ·57. | |
| „ reticulatus, *Schn.* | 1 | R. | ·50. | |
| Subfam. 2. *Boinæ.* | | | | |
| Boa constrictor, *L.* | 2 | R. | ·50, & 58. | * |
| Enygrus carinatus, *Schn.*, ♀ | 1 | R. | ·75. | |
| „ „ (young) | 4 | R. | ·60. | |
| Epicrates cenchris, *L.* | 1 | R. | ·62. | |
| Eryx johnii, *Russ.* | 1 | R. | ·57. | * |
| „ jaculus, *L.* | 1 | R. | ·40. | * |
| Fam. IV. Xenopeltidæ. | | | | |
| Xenopeltis unicolor, *Reinw.* | 1 | R. | ·45. | * |
| Fam. V. Ilysiidæ. | | | | |
| Ilysia scytale, *L.* | 1 | R. | sm. rud. | |
| Cylindrophis rufus, *Laur.* | 2 | R. | rud. | |
| Fam. VI. Uropeltidæ. | | | | |
| Rhinophis blythii, *Kel.* | 1 | R. | rud. | |

[1] The names in the following lists represent the species so described in the latest edition of the British Museum Catalogues of Snakes and Lizards, the specimens having been kindly identified for me by Mr. G. A. Boulenger himself. Thus a reference to those Catalogues will tell the reader what animal is meant, if he is in doubt. In some cases, however, I have added, in brackets, commonly used synonyms.

[2] I only give the Snakes which I have myself examined. Some of these have been previously examined for the lungs by Prof. Cope (these I have marked *), and a number of other species will be found in his paper (7).

[3] In these elongated forms, with rare exceptions, such as *Pygopus*, the other dimensions of the lungs vary roughly in proportion to the length.

In these lists "rud." signifies that the smaller lung is so small, not more than $\frac{1}{10}$ the length of the larger, and usually much less, that it can be of no appreciable use.

Sm. rud. (small rudiment) signifies that extra care will be needed to find the rudiment, as by cutting open the trachea as advised by Cope, (7) p. 224, so as to find its internal orifice.

A line thus —— signifies that I have not found a rudiment.

| | | | | |
|---|---|---|---|---|
| Fam. VII. COLUBRIDÆ. | | | | |
| Series A. AGLYPHA. | | | | |
| Subfam. 1. *Acrochordinæ.* | | | | |
| Chersydrus granulatus, *Schn.* | 1 | R. | ——— | * |
| Subfam. 2. *Colubrinæ.* | | | | |
| Tropidonotus natrix, *L.* | 14 & Em. | R. | sm. rud. | |
| Zamenis gemonensis, *Laur.* | 4 & Em. | R. | smallest [trace. | |
| Coluber (Elaphis) quatuorlineatus, *Lacép.* | 2 & Em. | R. | sm. rud. | |
| „ (Compsosoma) melanurus, *Schleg.* | 1 | R. | rud. | |
| „ (Pituophis) catenifer, *Blainv.* | 1 | R. | ——— | |
| „ longissimus, *Laur.* | 3 | R. | sm. rud. | |
| Ablabophis rufulus, *Licht.* | 1 | R. | ——— | |
| Lycophidium capense, *Smith* | 1 | R. | ——— | |
| Dendrophis pictus, *Boie* | 4 | R. | sm. rud. | * |
| Lystrophis (Heterodon) d'orbignii, *D. & B.* | 2 | R. | ——— | * |
| Heterodon platyrhinus, *Latr.* | 1 | R. | rud. | * |
| Coronella (Ophibolus) getula, *L.* | 2 | R. | ——— | * |
| Petalognathus (Leptognathus) nebulatus, *L.* | 1 | R. | sm. rud. | * |
| Liophis pœcilogyrus, *Wied* | 4 | R. | sm. rud. | |
| Oligodon sublineatus, *D. & B.* | 1 | R. | rud. | |
| Aspidura trachyprocta, *Cope* | 2 | R. | rud. | |
| Subfam. 3. *Rachiodontinæ.* | | | | |
| Dasypeltis scabra, *L.* | 1 | R. | sm. rud. | |
| Series B. OPISTHOGLYPHA. | | | | |
| Subfam. 4. *Dipsadinæ.* | | | | |
| Dipsas ceylonensis, *Gthr.* | 2 | R. | sm. rud. | |
| Cœlopeltis lacertina, *Wagl.* | 1 | R. | ——— | |
| Dryophis prasinus, *Boie* | 1 | R. | ——— | |
| Leptodeira rufescens, *Gm.* | 2 | R. | sm. rud. | |
| Psammophis crucifer, *Daud.* | 1 | R. | ——— | |
| Philodryas olfersii, *Licht.* | 1 | R. | sm. rud. | * |
| Subfam. 5. *Homalopsinæ.* | | | | |
| Homalopsis buccata, *L.* | 1 | R. | ——— | |
| Fordonia leucobalia, *Schleg.* | 1 | R. | sm. rud. | |
| Subfam. 6. *Scytalinæ.* | | | | |
| Oxyrhopus tergeminus, *D. & B.* | 1 | R. | sm. rud. | |
| Series C. PROTEROGLYPHA. | | | | |
| Subfam. 7. *Elapinæ.* | | | | |
| Elaps fulvius, *L.* | 1 | R. | ——— | * |
| „ hygeia, *L.* | 3 | R. | rud. | |
| Bungarus semifasciatus, *Kuhl* | 1 | R. | rud. | * |
| Subfam. 8. *Hydrophinæ.* | | | | |
| Hydrophis fasciatus, *Schn.* | 1 | R. | ——— | |
| Hydrus (Pelamis) platurus, *L.* | 1 | R. | ——— | |
| Platurus laticaudatus, *L.* | 1 | R. | ——— | * |
| Fam. VIII. AMBLYCEPHALIDÆ. | | | | |
| Amblycephalus boa, *Boie* | 1 | R. | rud. | |
| Fam. IX. VIPERIDÆ. | | | | |
| Subfam. 1. *Viperinæ.* | | | | |
| Vipera berus, *L.* | 3 | R. | ——— | |
| „ aspis, *L.* | 2 & Em. | R. | ——— | |
| „ arietans, *Merr.* | 1 | R. | ——— | |
| „ nasicornis, *Shaw* | 1 | R. | ——— | |
| Cerastes cornutus, *Forsk.* | 1 | R. | sm. rud. | |
| Subfam. 2. *Crotalinæ.* | | | | |
| Crotalus durissus, *L.* | 1 | R. | ——— | |
| „ horridus, *L.* | 1 | R. | sm. rud. | * |
| Trimeresurus wagleri, *Boie* | 1 | R. | rud. | |
| Bothrops atrox, *L.* | 1 | R. | ——— | |

| | Number of specimens examined. | Larger Lung. | Length of the Smaller Lung, that of the larger being taken as unity. |
|---|---|---|---|
| LACERTILIA. | | | |
| Fam. SCINCIDÆ [1]. | | | |
| Acontias meleagris, *L.* | 2 | R. | ♂ ·13; ♀ ·25. |
| ,, monodactylus, *Gray* | 1 | R. | ·40. |
| Scelotes bipes, *L.* | 1 | R. | ·83. |
| Fam. ANGUIDÆ. | | | |
| Anguis fragilis, *L.* | 4 | R. | ♂ ·62 & ·66; ♀ ·56 & ·96. |
| Ophisaurus (Pseudopus) apus, *Pall.* | 1 | R. | ·60. |
| ,, ventralis, *L.* | 1 | R. | ·33. |
| Fam. PYGOPIDÆ. | | | |
| Pygopus (Bipes) lepidopodus, *Lacép.* | 1 | R. | ·50 (but of equal stoutness). |
| Lialis burtoni (punctatus), *Gray* | 2 | R. | ·50. |
| Fam. TEIIDÆ. | | | |
| Ophiognomon abendrothii, *Ptrs.* | 1 | R. | ·50. |
| Fam. AMPHISBÆNIDÆ [2]. | | | |
| A. PROSPHYODONTES. | | | |
| Amphisbæna alba, *L.* | 2 | L. | ——— |
| ,, darwinii, *D. & B.* | 1 | L. | ——— |
| ,, fuliginosa, *L.* | 2 | L. | ——— |
| ,, ridleyi, *Blgr.* | 1 | L. | ——— |
| Blanus cinereus, *Vand.* | 2 | L. | sm. rud. |
| ,, strauchii, *Bedr.* | 1 | L. | rud. |
| Anops kingii, *Bell* | 1 | L. | ——— |
| Monopeltis magnipartita, *Ptrs.* | 1 | L. | rud. |
| Lepidosternon latifrontale, *Blgr.* | 1 | L. | rud. |
| ,, scutigerum, *Hempr.* | 1 | L. | rud. |
| B. EMPHYODONTES. | | | |
| Trogonophis wiegmanni, *Kaup* | 1 | L. | ·60. |
| Pachycalamus brevis, *Gthr.* | 4 | L. | ·25 to ·33. |
| AMPHIBIA.[3] | | | |
| Order GYMNOPHIONA. | | | |
| Fam. CÆCILIADÆ. | | | |
| Dermophis (Siphonops) mexicanus | 1 | R. | rud. |
| Ichthyophis glutinosus | 1 | R. | rud. |

[1] For footnotes, see opposite page.

## VII. On the Rationale of the Facts recorded in this Paper.

Taking these Snakes and Snake-like forms together, the facts noted in this paper are that while some agree with other air-breathing vertebrates in having two lungs well developed, some have one lung quite rudimentary or absent altogether, and that of these latter some have the right lung rudimentary or absent and some the left.

These facts suggest the questions—May we reasonably conclude that in the ancestors of all the different groups of pulmonate vertebrates the lungs were essentially similar in their first origin? If so, what was probably the most primitive condition? What significance may we attach to a divergence from such common condition of the kind above described?

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[1] I have also examined two specimens of *Lygosoma verreauxii*. In the first I was at first surprised to find the right lung apparently shorter than the left (contrary to the rule), but on further inspection I found that this condition was purely pathological, being due to the presence of a small tumour on the anterior border of the right lobe of the liver which interfered with the expansion of the lung. In a second specimen the lungs were of precisely equal length. This equality of the lungs in *L. verreauxii* and occasionally in *Anguis fragilis* (see list) makes me expect that (while the elongated snake-like form and the reduction or suppression of the limbs are commonly associated with the reduction of one lung) the lungs may be found equal in a number of the other elongated small-limbed lizards of which there are so many, especially in the family *Scincidæ*.

[2] J. von Bedriaga (Archiv für Naturgeschichte, 1884, Bd. i. p. 63) finds no trace of a second lung in *Blanus* (*Amph.*) *cinereus* and *B. strauchii* and *Trogonophis wiegmanni*; and C. Smalian (Zeitschrift für wissensch. Zool., Bd. xlii. pp. 188 & 189, 1885) finds no trace of a second in *A. fuliginosa*, *B. cinereus*, and *Anops kingii*, while as to *Trogonophis wiegmanni* he curiously prefers to regard it as having a bilobed single lung instead of a pair of lungs. Neither Bedriaga nor Smalian, so far as I have discovered, say which lung is well developed, but Bedriaga's figures of *B. cinerea* (*l. c.* pl. iv. figs. 2, 3) rightly represent it as the left.

[3] I have examined other Amphibia, especially the elongated forms with weak limbs and reduction of digits or absence of one pair of limbs (*Siren*); but in none of them can one lung be said to be atrophied as compared with the other. In most of them the two lungs are of equal length [*Siren lacertina*, *Menobranchus lateralis*, *Menopoma alleghanense*, *Salamandra maculosa*, *Triton cristatus*, *Amblystoma tigrinum* (fair-sized specimens of Axolotl)]. In a few cases there is a difference in the length. Thus in *Amphiuma* the right lung is the longer, while in *Proteus anguinus*, as is known from the published figures, the left is somewhat the longer, and the same appeared to be the case in some small specimens of Axolotl. These last two can hardly, however, be regarded as exceptions to the general rule, for we cannot say that the right lung is atrophied as compared with the left. Thus each lung of *Proteus* extends back to the ovary or testis, and the fact that the right lung is the shorter depends on the fact that in accordance with a common habit the right reproductive gland is situated further forward than the left. Again, though recording it for form's sake, I hardly think any stress should be laid on the right lung appearing shorter than the left in small (3 inches long) specimens of Axolotl. The lungs are equal in later stages, and the apparent difference in the younger specimens is probably due to the small intestine, which inclines to the right side, presenting the complete expansion of the terminal portion of the right lung, which projects backwards freely beyond the termination of the lung ligament.

The first two questions are very interesting, and I hope shortly to return to their discussion in another paper. For the present I may merely say that I incline to a view similar to that suggested by Goette in 1875, namely that the lungs have arisen from paired lateral branchial pouches [1].

Anyone who adopts this view will recognize a certain tendency to pairedness of the lungs as primitive. It seems, however, highly probable that lungs have arisen [from some such common anlage] independently in the different groups of vertebrates, and that we ought not to conclude that all pulmonate vertebrates are descended from a common pulmonate ancestor. To find such common ancestor we should perhaps have to go back to a time long before the first appearance of pulmonary respiration. It is thus quite conceivable, even accepting Goette's view, that in the ancestors of certain one-lunged types the branchial pouch of one side may have from the first remained rudimentary, that of the other side alone developing into a lung. Such a view is also quite in harmony with embryology; for in the embryos of such forms as *Vipera aspis* and *Typhlops lumbricalis* there is no trace of a second lung even in early stages. While, however, neither embryology nor the theory of homology with paired branchial pouches runs counter to the view that the ancestors of some pulmonates may from the first have had but one lung, while others had two, it seems to me that there are certain facts of comparative anatomy which are in favour of the view that in their first beginning the lungs were not only potentially but actually paired in the ancestors of many species which now have no trace of more than one.

Thus, as is well known, we find cases of two species of Snake which are so alike in other respects as to be classed in the same genus, one of which has a rudiment of the left lung, while the other has no trace of such [2]. Now the pesistence of the rudiment as such a definite structure in the adult, combined with the fact that the rudiment is of proportionally greater size in the embryo, suggest that it is the reduced remains of an organ which was once a functional lung. If, then, a functional lung can be reduced to a mere functionless rudiment, it seems likely, when we find two species of the same genus, one of which has such rudiment while the second has not, that in this second the reduction has but been

[1] The clue to my reason for taking this view is briefly this, that I find that in the Lizard, Snake, and Bird the œsophagus becomes separated off, from behind forwards, from the anlage of the lungs and from the trachea, just as it would appear from Nestler's observations the anlage of the œsophagus is separated off from the branchial chamber in the metamorphosis of *Ammocœtes* into *Petromyzon* [Nestler, 'Archiv für Naturgeschichte,' Jahrg. lvi. Bd. i. pp. 100–105]. From the best published accounts the same is true of the development of the œsophagus, lungs, and trachea of Amphibia and Mammalia.

[2] Thus in my list above *Crotalus horridus* has a small rudiment, while *C. durissus* has none; *Elaps hygeia* has a rudiment, while *E. fulvius* has none. Similarly, in Cope's paper (7) p. 223, we have such a difference recorded in two other genera besides *Crotalus*, viz. in *Bothrops* and *Ancistrodon*.

carried a step farther and that the ancestors of this second, like those of the first, had some trace of a second lung.

Secondly, what significance may we attach to the suppression of one or other lung? Can we, I mean, correlate such suppression with any other anatomical or physiological characters?

As we know, there is, as a rule, on the whole a very distinct bilateral symmetry in the bodies of pulmonate vertebrates, but there is also, as is well known, one marked departure from such symmetry which appears early, with which may, I think, be correlated certain departures from symmetry in some of the other organs. I refer to the marked leaning of the stomach to the left side. Whatever be the cause of this, we have the fact, as also the fact that in the case of these abnormal specimens in which the position of the stomach is reversed there is wont to be a reversed position of the great vascular trunks (the aortic root and the postcaval vein) and other correlated changes. There is, then, evidently a correlation between the asymmetry of the stomach and the asymmetry of some of the other organs; and while in some cases it may be better to say that both are due to some common cause, in other cases (and I think this difference in the size of the lungs one of them) it would seem reasonable to speak of the asymmetry of the stomach as a cause of the asymmetry in the other organ.

From the fact, however, that only some of the animals which have the asymmetrical stomach have unequal lungs, it is obviously not by itself a sufficient cause. The leftward inclination of the stomach and adjoining part of the œsophagus only leads to inequality of the lungs when some second cause, such as the snake-like habit of the body [which naturally renders the accommodation of the viscera a work of greater difficulty], or in mammals some other cause [which I will presently suggest], is superadded.

This view harmonizes with the fact that in the Amphisbænidæ [in which the left lung is the larger] the leftward displacement of the stomach is but small, while the œsophagus is sometimes markedly displaced to the right side. Of course this, as it stands, might suggest that we had here merely a case of mechanical displacement of the œsophagus and stomach by the left lung instead of an obliteration of the right lung by the rightwardly inclined alimentary canal. But in certain of the Amphisbænidæ [e.g. *Amphisbæna alba* and *Anops kingii*, two forms with a total absence of right lung] it is clear that we have something more than this, for though we have no case of "situs inversus" of the postcaval vein, which runs as usual on the right side, we find that the veins from the stomach to the liver are not as usual confined to the median gastro-hepatic ligament, but run in that right dorsal ligament of the liver (the "Hohlvenengekröse" mentioned above, p. 698) which usually carries none but systemic veins, such as the postcaval and vertebro-intercostals. It is at least interesting that this, so far as I am aware unique, feature of the vascular system, which, I take it, argues that the stomach is morphologically more to the right side than usual, should be found in (some, not all of) the Amphisbænidæ, which are also unique in having the right lung partially or completely suppressed[1].

With regard to the lungs of mammals—it has been suggested by some[2] that this inequality is due to the unsymmetrical position of the heart. There are, however, certain considerations which induce me to incline to another view[3]. Firstly, the lungs may, as we have seen, differ markedly in size in reptiles in which the heart is symmetrically situated. Secondly, in the few mammals which I have examined the smaller size of the left pleural space seems to depend not so much on the position of the heart as on the want of symmetry in the mediastinal membranes, whose line of attachment to the diaphragm is a curve sweeping round the left border of the central tendon. Thus perhaps the first cause of the inequality of the lungs here, as in Snakes, may have been the leftward displacement of the stomach,—which cause, however, may have only come into action when, with the development of the diaphragm, the mediastinum came to be *fixed* in its oblique left-sided position. According to this view the unsymmetrical position of the heart would be due to the same cause as the inequality of the lungs, and not be itself the cause of this.

## VIII. Conclusions.

1. In all the Amphisbænidæ examined the right lung is either absent or smaller than the left.

2. In all the other vertebrates examined the right lung is fully developed, and if one lung is rudimentary or absent, it is the left. Thus ———

3. The left lung is the smaller in many mammals, and more markedly so in the Gymnophiona and many snake-like Lizards [not Amphisbænidæ] and Snakes, in which last the left is usually reduced to a mere rudiment or absent altogether.

4. In the more theoretical section VII. I incline to the view that in their first beginnings the lungs were in the ancestors of all air-breathing vertebrates potentially paired, having their origin in paired branchial pouches, and show reason to believe that they were actually paired in the ancestors of at least some forms which show no trace of a second.

5. It would seem that the primary cause of the inequality of the lungs, where it occurs, is that one-sided displacement of the stomach and adjoining portion of the œsophagus which is seen in

[1] To avoid needless repetition, other remarks which naturally might follow here are placed only in the next section (Conclusions 5 and 6)

[2] G. L. Duvernoy, 'Leçons d'Anat. comp. de G. Cuvier,' 2nd ed. tom. vii. pp. 20, 24, 25 (1840).
R. Owen, 'Anatomy of Vertebrates,' vol. iii. p. 577 (speaking of Marsupials) (1868).

[3] I refer only to the leftward displacement of the ventricle. I do not dispute the fact that in most mammalian lungs we note that the left bronchus appears the longer, owing apparently to the fact that the one-sided development of the aortic root has entailed the suppression of part of the left lung in that region.

nearly all air-breathers, but that this only leads to inequality when some secondary cause, such as the acquisition of a slender snake-like habit of body (or in mammals some other cause, see § VII.), is superadded. Moreover, it would appear that in some cases (as in most Snakes), the inequality once started, the replacement of paired lungs by one larger one has in its turn led to a further displacement of the alimentary canal and other organs.

While thus suggesting an order of priority for correlated modifications, the writer does not lose sight of the fact that these modifications have all arisen under the supervision of Natural Selection, and that the safest and most philosophical course is simply to say that the aggregate of modifications are in some way more or less advantageous.

6. The question occurred to me whether the complete or partial suppression of the right lung peculiar to Amphisbænidæ might serve to tell us anything as to the stage in their evolution at which the Amphisbænidæ branched off from the stock common to them and other Lizards—whether, for instance, it might indicate that they branched off before their common ancestors had acquired lungs, at a time, therefore, when perhaps the respective ancestors of existing Lacertilia and Amphibia had diverged comparatively little

However, on consideration it seems clear that the facts here recorded do not by themselves prove any such thing, and that they are not by themselves inconsistent with a considerably later separation of the Amphisbænians.

7. This peculiarity of the Amphisbænian lungs is for the present, then, but one added to the list of the peculiarities of these very interesting animals; but the fact that (so far I have been able to ascertain) no other vertebrate has the right lung suppressed, suggests that this at first sight unimportant character may be found to be correlated with some other character the significance and importance of which may be more obvious.

## IX. Bibliography [1].

(1) Chr. Lud. Nitzsch. De Respiratione Animalium, p. 13. Vitebergæ, 1808.

(2) J. F. Meckel. "Ueber die Respiration der Reptilien." Deutsches Archiv für die Physiologie, Bd. iv. pp. 60–89 [especially p. 84] and plate 2 [of which the explanation is given at the end of Heft 1, pp. 162–164]. Halle, 1818.

(3) J. F. Meckel. System der vergleichenden Anatomie, Bd. vi. pp. 257–262 [especially pp. 257 and 260]. Halle, 1833.

(4) Leçons d'Anatomie comparée de Georges Cuvier, rédigées et publiées par G. L. Duvernoy. 2nd ed., tom. vii. pp. 19–163. Paris, 1840.

[1] Milne-Edwards (6) refers to a separate paper by Lereboullet entitled 'Anatomie comparée de l'appareil respiratoire.' None of the London Libraries accessible to me possess a copy of this paper; so I have not been able to see it, and consequently do not put it on the list, but it is possibly quite as worthy of a place there as some of the others.

(5) H. Stannius. 'Handbuch der Anatomie der Wirbelthiere' [2nd part of the 'Handbuch der Zootomie' by v. Siebold and Stannius]. 2nd ed. 2nd part, pp. 206–208 [with their footnotes]. Berlin, 1856.
(6) H. Milne-Edwards. Leçons sur la Physiologie et l'Anatomie comparée de l'Homme et des Animaux. Tom. ii. pp. 307–313 [and their footnotes]. Paris, 1857.
(7) E. D. Cope. "On the Lungs of Ophidia." Proc. Amer. Phil. Soc. vol. xxxiii. pp. 217–224, pls. xi.–xvi. 1894.
(8) E. D. Cope. "On the Classification of Snakes." Amer. Naturalist, Oct. 1894, pp. 831–844, pls. xxvii. & xxviii.

## X. EXPLANATION OF PLATE XL.

*A.* Artery.
*Ao.* Dorsal aorta.
*Œsoph.* Œsophagus and anterior part of stomach.
*Rt. & Lt.* Right & Left.
*V.* Vein.
*V.c.p.* Vena cava posterior.
*V.P.* Portal vein.

Fig. 1. Heart, lungs, œsophagus, and anterior part of liver of *Heterodon platyrhinus*, seen from ventral side.

Figs. 2, 3, and 4. Transverse sections of *H. platyrhinus*, seen from behind.—Fig. 2 through heart; Fig. 3 through fork of trachea and left lung Fig. 4 through liver-region.

Figs. 5–9. Transverse sections of different Snakes through liver-region, all seen from behind:—
Fig. 5. *Platurus laticaudatus.*
Fig. 6. *Python reticulatus.*
Fig. 7. *Tropidonotus natrix.*
Fig. 8. *Vipera berus.*
Fig. 9. *Dryophis prasinus.*

Fig. 10. Semidiagrammatic view of part of trunk of a two-lunged Snake. The right-hand end, which is seen in section, is the posterior end. The body-wall of the left side is supposed cut away so as to show the various series of blood-vessels which run between the vertebral column and the liver, separating the two lungs.

## 2. Observations on the Frilled Lizard, *Chlamydosaurus kingi*. By W. Saville Kent, F.L.S., F.Z.S., &c.

[Received October 23, 1895.]

(Plate XLI.)

The Frilled Lizard, *Chlamydosaurus kingi*, is a native of the Northern or tropical districts of Australia, occurring in tolerable abundance in both the Eastern, or Queensland, and the North-western districts of that island-continent. The habits of the species are essentially sylvan, its favourite haunts being the more or less thickly wooded scrub-lands, and its chief resort the trunks and lower limbs of the larger trees. The most remarkable structural feature of *Chlamydosaurus*, and from which it derives its popular title, is, as recorded in its earliest description by Dr. J. E. Gray in the Natural History Appendix to Captain King's 'Survey of the Coasts of Australia,' vol. ii. 1826, the extraordinary development of the cuticle in the neighbourhood of the neck.